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A Survey for Grasshopper Parasites in Temperate South America

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Introduction

In 1937-38 the Argentine Department of Agriculture initiated an exchange of grasshopper parasite material with the Canadian Department of Agriculture which was engaged in a study of the natural control of grasshoppers in various provinces of Canada. By 1942 it was considered desirable to introduce exotic species of parasites into Canada on as wide a scale as possible, and the temperate regions of South America were selected as being the most promising for a survey. The parts of the temperate zone of South America to which preferential attention was to be given included the countries of Uruguay, Argentina, and Chile. The well known grasslands of the Rio de la Plata area have been partially transformed into one of the world centres for cereal production and as in other parts of the world increased grasshopper populations constitute a major problem in the agriculture of the region. Here species of the genus *Dichroplus* are frequently pests in the way in which members of the closely related *Melanoplus* are in North America.

The main commercial grain belts of Uruguay and Argentina are concentrated in relatively small areas of the national territories of these countries, and the economy of both is orientated to give greater emphasis to livestock ranching with its stress on pasture and alfalfa. In Uruguay the cereal belt is restricted to a strip approximately 50 miles wide bordering the Plata estuary on the south and southwest; the country to the north and east of this is broken by grass covered hills of subdued contour which merge into the hilly uplands and plateaus of southern Brazil. The predominant vegetation here is a prairie of tall grass, similar to parts of the Argentine Pampa, and it is in this section of rolling topography that the heavy populations of grasshoppers are found.

The great central cereal and livestock zone of Argentina occupies most of the Provinces of Santa Fe, Cordoba, Buenos Aires, and part of the Territory of La Pampa (Plate I). It is bounded on the south by the arid, wind swept plateaus of Patagonia, on the north by the semi-tropical undeveloped Chaco, and on the west by desert and the Andean piedmont. This is the famous Pampa; an area with an extension of approximately 500 miles north and south and 250 miles east and west. The entire zone is extremely flat, the only conspicuous hills rising above the plains being the Sierra del Tandil (1,600 ft.) and Sierra de la Ventana (4,000 ft.) in the south. It is customary to recognize a drier western part of the Pampa and it is in the poorer pasture lands of this region, particularly in the southwest, that grasshopper populations attain their maximum intensities. Agriculture to the west and south of this central zone is largely restricted to irrigated valleys such as that of the Rio Negro crossing Patagonia or favourable areas in the semi-arid strip along the foothills and lower slopes east of the Andes. Grasshopper infestations here are sometimes severe but usually of very localized distribution, and do not in any way constitute a problem of the magnitude of that in parts of the Pampa.

It will be realized that in regard to topography and climate the wheat belt of Argentina and Uruguay is quite different from that of the prairies of western

PLATE 1

Canada. It lies in latitudes corresponding to those of Georgia and South Carolina. The climate of the region resembles east Texas, and in both cases there is the transition to a steppe climate as one proceeds westward. The tapering land form of southern South America with its resultant subjection to oceanic moderating influences is characterized by a much milder climate than that obtaining in similar North American latitudes; there is no part outside the high Andes with winters comparable in severity to those of Canada. Griffith Taylor

(1950) considers that homoclimes—defined as regions of similar climate—of the prairies from Winnipeg west to Calgary and Lethbridge are found only in Russia at stations such as Kazan in the plains west of the Urals. The same author compares the dry interior of British Columbia around Kamloops to inland sections of southern Chile. A better approximation to these British Columbian conditions would appear to be found in the dry foothills of the Argentine southern Andes south of latitude 40°. This summer dry semi-arid strip of Patagonia, shut off from the moisture bearing westerly winds, is sometimes compared to the North American Great Plains. The dissimilarities are appreciable, and this is reflected in the relatively poor cultivation of crops in the South American region. Nevertheless it was considered advisable to give major attention to those sections of South America where physical conditions are closest to those of the high latitudes of Canada.

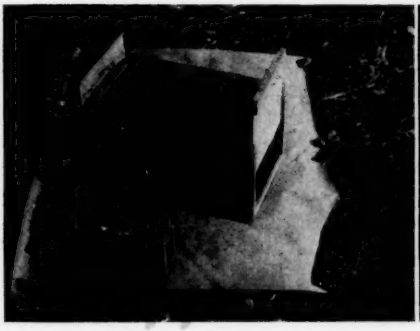

FIG. 1a

FIG. 1b

Procedure

Since the territory suitable for survey was very extensive and involved international boundaries and distances up to a thousand miles it was not possible to organize the work from one centre. Convenient towns or villages were established as headquarters for a given season and field collections made within a radius of one to two hundred miles of any such point. Grasshopper samples were secured by sweeping with nets, and supplemented in some seasons in western Patagonia by purchase at one or two Argentine cents apiece from casual collectors who caught specimens by hand. Whenever practicable these collections were made regularly throughout the season at definite sampling stations. Material being swept in the field was retained in small, specially constructed, plywood cages measuring 8 ins. by 4 ins. by 4 ins. with one or more sides formed of very narrow gauge mesh wire to hold any emerging parasite larvae (Fig. 1a). This type of cage has been used extensively over many years in investigations by the Argentine Ministry of Agriculture on the locust *Schistocerca cancellata* Serv. Grasshoppers were introduced into these cages through a small hole bored in the top wooden surface, the hole being closed by an ordinary cork stopper. With careful handling it was found that these containers could be used to hold about 200 specimens of the *Dichroplus* species for periods up to four hours without undue mortality, although as a measure of safety such collections were always transferred as soon as possible to the large rearing cages maintained at the seasonal field headquarters. Assistants employed throughout a season were trained to separate and cage apart the various grasshopper species as they were being collected by nets, etc. in the field but this procedure was not

possible with the more casual workers and separation was effected later in the large laboratory cages in such cases.

These large cages were of lightweight but strong construction, and were of the type shown in Fig. 1, b. They were designed in such a way as to be easily and completely dismantled with a view to facilitating storage and transportation from one field headquarters to another. This was achieved by making the supports with a system of mating grooves and flanges. The cages measured 20 ins. by 10 ins. by 9 ins., with the top, bottom, and side pieces consisting of fine mesh wire of 15 inch gauge. The cages were placed on end and one of the solid end pieces slid up for the periodic introduction of grasshoppers. The mesh wire floor of the cages was painted black to show up emerging parasite larvae. A thousand adult grasshoppers could be handled easily in one of these cages and at times as many as 2,000 were held without excessive mortality. Twenty-four such cages were constructed so that samples of 25,000 or more hosts could be handled at any one time.

The cannibalistic tendency of the grasshoppers to eat dead or dying specimens under these somewhat crowded conditions was effectively controlled by cleaning the cages daily and supplying ample, fresh food in the form of leaves of lettuce or cabbage, or occasionally alfalfa. All rearing was done in rooms with no temperature control, the usual procedure being to allow room temperatures to fall to the lowest possible level overnight by leaving windows, etc. open, and then cleaning, feeding, and removing parasite maggots in the earlier hours of the morning before the grasshoppers became too active to permit opening of the cage end pieces. Hosts were kept in these cages for 15-20 days depending on the prevailing temperatures and the incidence of emerging dipterous maggots. Dead host specimens were removed daily to numbered glass jars or tins placed on the corresponding cages and retained there for several days for possible parasite emergence before being preserved or finally discarded. The dipterous larvae were held for transformation or hibernation in small two inch diameter salve tins containing a mixture of earth and sand.

Field Collections and Parasitism

No attention was given in the present survey to natural enemies of grasshopper egg pods. Investigations by various South American students suggest that in the temperate part of that continent such parasites and predators as occur are of little importance. As adults, some meloids of the genus *Epicauta* are major vegetable pests. In the larval stages these species undoubtedly destroy vast numbers of grasshopper eggs each year, but the destructive high adult populations of the acridids continue annually. Bombyliidae and Scelionidae are virtually unrecorded as grasshopper enemies and only within the past two years has a member of the latter family been observed by entomologists of the Argentine Ministry of Agriculture.

Argentine workers have recorded an appreciable list of parasites of nymph and adult grasshoppers and locusts in that country and Chile (Lahille 1907, Blanchard 1933, 1939, 1942, 1943, 1951, Salavin and Crouzel 1942). Stuardo (1946) in his catalogue of Chilean Diptera cites the sarcophagids *Acridiophaga caridei* Brethes, *A. ebi* Hall, *A. lorosa* Hall, *Protodexia australis* Blnchd., and *Protodexia quaesita* Hall, but gives no indication of host relationships. The following diptera have been reared from members of the genus *Dichroplus* in which the major pest grasshoppers are included.

Sarcophagidae

Protodexia australis Blnchd.
Protodexia liebermanni Blnchd., i.l.

Protodexia aleuaphaga Blnchd.
Tephromyiella neuquenensis Blnchd.
Opsophyto arteagai Blnchd.
Sarcophagulopsis trigonophymi Blnchd.
Hypopelta salavini Blnchd., (*in litt.*)
Acridiophaga caridei Brethes

Tachinidae

Ceracia subandina Blnchd.
Ceracia maldonadoi Blnchd.

Nemestrinidae

Neorhynchocephalus sulphureus Wied.
Neorhynchocephalus vitripennis Wied.

The migratory locust *Schistocerca cancellata* was thought by earlier workers such as Lahille to be attacked by a large number of dipterous parasites. This list was reduced to two species, *Acridiophaga caridei* and *Doringia acridiorum* Weyenburgh, by Blanchard (1933) who has since eliminated the latter species as being a scavenger which occasionally attacks sickly or dying specimens presumably after the manner of *Sarcophaga destructor* Malloch on *Schistocerca gregaria* Forsk., (Wood 1933). Subsequently the fly *Opsophyto arteagai* has been found as a true parasite of *Schistocerca*, but on the basis of later work there seems little doubt that early investigators of the natural enemies of this locust not only misjudged the status of most diptera associated with it but also overestimated the controlling function of the few true sarcophagid parasites.

A few relatively uncommon solitary grasshoppers are also known to be attacked by sarcophagids. These are *Diponthus* sp., *Elaeochlora viridicata* (Serv.) Stal., *Zoniopoda cruentata* Blanch., and *Anchocoema ogloblini* M. Letao, parasitized respectively by *Protodexia diponthi* Blnchd., *Protodexia crouzeli* Blnchd., *P. deaurata* Blnchd., and *P. ogloblini* Blnchd. Most of these parasites are from hot dry desert areas such as Cordoba, climatically very distinct from Canadian conditions.

The most abundant grasshoppers of Uruguay and Argentina are members of the subfamilies Cyrtacanthacridinae and Acridinae. They include the following species.

Acridinae

Scyllinops bruneri Rehn.
Scyllinops pallida (Bruner) Rehn.
Scyllina variabilis Bruner

Cyrtacanthracridinae

Schistocerca cancellata Serv.
Dichroplus maculipennis (Blanch.) Lieb.
Dichroplus pratensis Bruner
Dichroplus elongatus G. Tos.
Dichroplus conspersus Bruner
Dichroplus punctulatus Thunberg
Dichroplus bergi Stal.
Dichroplus vittatus Bruner
Dichroplus vittiger (Blanch.) Berg
Dichroplus democraticus (Blanch.) Lieb.

The subfamily Oedipodinae, in which is placed the well-known *Camnula pellucida* Scudder, is represented by *Trimerotropis pallidipennis* (Burm.) Sauss. This species is distributed throughout temperate South America, but its incidence is very low and its habitat is in the arid zones.

The Acridinae listed above are sometimes the dominant group on poorer grasslands and are particularly abundant in central Uruguay where the extensive open ranges are used only for livestock ranching. However, little attention was given to this *Scyllina-Scyllinops* complex after preliminary sampling showed no parasitism, while it was also considered unlikely that any possible parasites of these small grasshoppers would be of utility against the larger Canadian *Melanoplus*. Similarly, parasitism of the migratory locust *Schistocerca cancellata* was only briefly studied.

In the open ranges of Uruguay and Argentina the grasshopper swarms consist of varying proportions of the forementioned *Dichroplus* species. The forms *D. vittiger* and *D. democraticus* are restricted to Southern Chile and the mountain valleys of southwestern Patagonia. Excluding from consideration *S. cancellata*, the "tucura" *D. maculipennis* is regarded as the major pest, and is particularly harmful in the southwestern parts of the Province of Buenos Aires. Here swarms frequently spread from pasture to cultivated plants (Drake and Richardson, 1940). This species is virtually absent from sections such as the Provinces of Santa Fe and Entre Rios, Argentina, where *D. pratensis* or *D. elongatus* are occasionally abundant; and from Uruguay where its place is taken by the species *D. pratensis* and *D. conspersus*. Numerous foci of infestations of the different *Dichroplus* species are indicated in the systematic and distributional studies of the grasshoppers of the various provinces of Argentina being made by Liebermann (1938, 1939, 1940, 1941, 1945).

Selection of the general areas to be worked was decided after consultation with officers of the local Departments of Agriculture, and after an examination of published data on the grasshopper and parasite faunas (Liebermann, loc. cit., Schiuma 1938, Trujillo 1942, Ruffinelli and Carbonell 1944, Blanchard 1939, 1942). As indicated in the introduction preferential attention was given to those areas of Argentina which most closely approached the latitudes of the Canadian western wheat belt. Field headquarters for rearing were established at Montevideo, Uruguay, and Buenos Aires and El Bolson, Argentina. Rearing work at Buenos Aires was handled by staff of the Argentine Laboratorio Central de Acridiologia, which was studying the parasitism of collections of grasshoppers sent in by one of their field workers from the province of Buenos Aires. Besides avoiding duplication of survey this collaboration allowed the author to make extensive field excursions in areas outside the field of activity of the Laboratorio Central. Unfortunately it was found that lack of transportation facilities from outlying districts resulted in a very heavy mortality in the grasshopper samples forwarded for examination, and after one season this procedure was therefore abandoned.

The location of the sampling stations is shown on the map, and the overall parasitism by diptera of the seasonal collections at different points in Uruguay and Argentina is given in Tables 1 and 2. All host samples taken within a five mile radius of any of the points indicated have been grouped together to form the figures for any one such location. The Canadian procedure of determining the parasitism by dissection was not followed in the present survey; the figures for the percentage parasitism are based on an assumed average emergence of two larvae per host, an estimate probably giving somewhat liberal figures of percentage parasitism since from one to ten larvae of the various sarcophagid parasites can successfully develop in the hosts. The author realizes that figures of percentage parasitism are of questionable value when used without reference to the nature and dynamics of the host populations. But there is, as yet, no satisfactory sampling technique for evaluating the effect of parasites on a very

fluid insect population of the grasshopper type, and its elaboration scarcely falls within the field of foreign parasite exploration. Meanwhile, reliance must be based on estimates expressed in general terms, one of which is percentage parasitism.

It will be seen from an examination of the tables that the parasitism of the samples for a season at all stations was invariably low, and this irrespective of host densities. In many instances the low parasitism occurred in stations where observations were carried out over a period of three or four years, and there appears no reason to believe that any of the parasites present are at any time very effective as controlling agents. It was unusual to find one of the host samples, which were taken at regular fortnightly intervals throughout the season at some locations, with a parasitism of 25%, a low figure compared with other published records. Even this figure was only reached in very restricted areas and on one or two occasions in the summer. Thus in stations such as El Bolson and Hoyo de Epuyen, Argentina, these maxima occurred about mid January and March, and appeared to be related to the two periods of major activity of the adult sarcophagids. In this area flies from the overwintering generation of larvae are active in the field in late December and early January, while flies of the partial second generation are active in the latter part of February and early March. However, in a general assessment of the results of the present series of observations, involving examinations of approximately 320,000 grasshopper hosts of the *Dichroplus* group and some 40,000 of the *Scyllinops* complex, it cannot be claimed in any single instance that the action of the sarcophagids and other parasites was of value in suppressing an infestation. This discouraging feature stands out in any general consideration of the effect of parasites on the grasshopper populations of the South American areas investigated. Where ecological conditions are especially favourable, North American experience has shown very effective localized parasite action in certain instances. The failure to observe similar occurrences in Uruguay and Argentina over a six year period is somewhat surprising. It was thought that, in the case of some low host infestations in the Bolson-Esquel section of Argentina, removal of part of the parasite populations by early season sampling might be partially responsible for such results. This aspect was examined by leaving undisturbed selected sampling points until late in the season. No significant difference was observed between these and other points.

In areas fringing the Argentine southern Andes where there remain tracts of the primitive vegetation despite an increasing pressure from agricultural development, parasitism of the grasshopper infestations was better both qualitatively and quantitatively than that obtaining in the open pampa type of habitat. This is supported by unpublished data of the Argentine Laboratorio Central de Acridiologia showing that the parasitism in locations such as Buenos Aires province is always inferior to that of the valleys of southern Argentina and Chile. This difference has been attributed to the greater abundance in such areas of wild flowers which serve to feed dipterous adults, but it seems probable that the higher parasitism is a reflection of the general undisturbed nature of such environments with their limited grasshopper infestations of relatively low intensities. At the same time it must be recognized that the position in the open grass steppe habitat of the type represented by the stations Zapala, Maiten, and Cholila situated in the southern territories of Neuquen, Rio Negro, and Chubut, was poor in respect to both grasshopper and parasite faunas.

The complex of the parasite species attacking the swarms varied from point to point. Their incidence at the different sampling stations of Uruguay

TABLE 1. ESTIMATED PERCENTAGE PARASITISM* BY DIPTERA OF DICHROPLUS COLLECTIONS AT STATIONS IN URUGUAY 1943–44.

Locality	1943		1944	
	Host Sample	Percent Parasitism	Host Sample	Percent Parasitism
1. Santa Isabel	—	—	9840	4.4
2. Parish	—	—	1145	0.5
3. Villasboas	5030	0.3	2795	0.5
4. Durazno	195	0	1185	0.2
5. Goni	1170	0	700	0.9
6. Sarandi Grande	2310	2.1	300	3.3
7. Trinidad	—	—	375	0.3
8. Mal Abrigo	—	—	210	0
9. Arroyo Grande	—	—	105	0
10. Cardona	—	—	460	0
11. Colla	—	—	95	0
12. Rosario	—	—	250	0

* Based on an emergence of two larvae per host.

TABLE 2.—ESTIMATED PERCENTAGE PARASITISM* BY DIPTERA OF DICHROPLUS COLLECTIONS AT STATIONS IN ARGENTINA 1945–49.

LOCALITY	1945		1946		1947		1948		1949	
	Host Sample	Percent para-ism	Host Sample	Percent para-ism	Host Sample	Percent para-ism	Host Sample	Percent para-ism	Host Sample	Percent para-ism
1. General Lamadrid	2000	4.0	—	—	—	—	—	—	—	—
2. Ing. Huergo	700	3.0	—	—	—	—	—	—	—	—
3. Manique	600	1.0	—	—	—	—	—	—	—	—
4. Zapala	4220	1.4	—	—	—	—	—	—	—	—
5. Bariloche	900	0	—	—	—	—	—	—	—	—
6. El Bolson	5250	2.3	10880	2.2	10705	3.4	17660	6.2	16060	2.6
7. Lago Puelo	—	—	16750	4.2	12785	8.1	8065	4.0	—	—
8. Rio Turbio	—	—	—	—	—	—	1350	0	—	—
9. Hoyo de Epuyen	—	—	1130	4.0	9260	5.2	20780	7.8	1415	5.6
10. Los Repollos	—	—	11300	4.7	58065	2.5	32150	2.7	44155	0.7
11. El Maiten	—	—	—	—	340	0	—	—	—	—
12. Cholila	—	—	—	—	—	—	—	—	1420	1.5

* Based on an emergence of two larvae per host,

and Argentina is indicated in the following list. No parasitism was observed in eight localities given in Tables 1 and 2 but omitted from this list.

Santa Isabel	*Protodexia australis* (Sarcophagidae); *Neorhynchocephalus* spp. (Nemestrinidae); sp. X. (Mermithidae)
Parish	*P. australis*; *Neorhynchocephalus* spp.; sp. X.
Villasboas	*P. australis*; *Neorhynchocephalus* spp.; sp. X.
Durazno	*P. australis.*
Goni	*P. australis.*
Sarandi Grande	*P. australis.*
Trinidad	*P. australis.*
General Lamadrid	*Opsophyto arteagai* (Sarcophagidae)
Ing. Huergo	*P. australis*; *P. aleuaphaga* (Sarcophagidae); *Neorhynchocephalus* spp.
Mainque	*P. australis*; *P. aleuaphaga* (Sarcophagidae); *Neorhynchocephalus* spp.

Zapala	*P. australis*; *Neorhynchocephalus* spp.
El Bolson	*P. australis; P. liebermanni; Tephromyiella neuquenensis; Acridiophaga caridei*; *Hypopelta salavini*; Sp. Y. (Sarcophagidae)
Lago Puelo	*P. australis*; *P. liebermanni*; *T. neuquenensis*; *A. caridei*; Sp. Y.
Hoyo de Epuyen	*P. australis*; *P. liebermanni*; *T. neuquenensis*; *A. caridei*; Sp. Y.
Los Repollos	*P. australis*; *P. liebermanni*; *T. neuquenensis*; *A. caridei.*
Cholila	*P. australis*; *P. liebermanni*; *T. neuquenensis.*

It will be seen that the foregoing includes all species recorded as parasitizing *Dichroplus* in Uruguay and Argentina with the exception of *Sarcophagulopsis trigonophymi* from Buenos Aires province, and the *Ceracia* spp. from Patagonia and northern Argentina. The failure in the present survey to secure *Ceracia subandina* Blnchd. from Patagonia was puzzling though it should not be overlooked that the specimens secured by the Argentine entomologists were from localities near Comallo situated in a complete 'desert' zone. This zone was not investigated by the writer. The species *Tephromyiella liebermanni* is at present known only from Chile.

Of the sarcophagids the species *P. australis* and *P. liebermanni* were easily dominant in areas where a group of parasites occurred, effecting at least 80% of the parasitism of the host. These were followed in importance by *T. neuquenensis* and *A. caridei*, while *O. arteagai* was peculiarly local in its distribution and apparently not very effective in the pampa habitat since in subsequent years it has only been obtained infrequently by the Laboratorio Central de Acridiologia. Only a single specimen of *Hypopelta salavini* was secured. The species *A. caridei* is known to effect a high parasitization of its usual host *Schistocerca cancellata* in restricted areas, but it appears to be singularly ineffective against the solitary grasshoppers although it has been repeatedly reared from three *Dichroplus* species and even from the small specimens of *Scyllinops* group.

In the present survey the beeflies, *Neorhynchocephalus* spp., were very rare in Uruguay, but at Ing. Huergo and Mainque in the Rio Negro valley of Argentina they parasitized up to 3% of small samples of *D. elongatus* collected from alfalfa fields. Adult flies were often seen in flight in these fields. Crouzel and Salavin (1942) report figures of parasitism up to 16% from parts of this same valley, and as high as 35% from points near Buenos Aires.

In the late summer the undetermined nematode of the family Mermithidae was found parasitizing as much as 20% of the hosts in small samples of grasshoppers from central Uruguay. Such parasitism, however, was not representative of the general position there in mid season, but the results of the collections did suggest that at least in some stations this nematode was a more effective mortality factor than the combined action of the sarcophagids and nemestrinids. In this connection it should be pointed out that Schiuma (1938) stated that in the early summer of 1937 a mermithid, probably *Hexamermis acridiorum* Weyenbergh, parasitized 70-90% of grasshopper samples from sections of La Colina and Lamadrid, southwestern Buenos Aires province, Argentina, though in a later communication with Liebermann (1946) the same author observes that in subsequent years there had been a great decrease in the nematodes in that area. Dr. Gutierrez, specialist in Helminthology at the Ministry of Agriculture, Buenos Aires, recently informed the writer in conversation (1949) that at least three genera of mermithids are parasitic in grasshoppers in the River

Plate area. One of these species was stated to be *Agamermis decaudata* Cobb, Steiner. Christie.

Biology of the More Important Parasites

The publication of Blanchard (1951) should be consulted for details of the host preferences of the recorded dipterous parasites in Uruguay, Argentina, and Chile. Here reference will be made only to the four principal parasites encountered in the present survey, and on which some biological observations were made. These are *Protodexia australis*, parasitizing adult *D. maculipennis*, *D. pratensis*, *D. conspersus*, and *D. elongatus*; *P. liebermanni* parasitizing adult *D. maculipennis*, *D. pratensis*, and *D. democraticus*; *Tephromyiella neuquenensis* parasitizing adult *D. maculipennis*, *D. pratensis*, *D. elongatus*, *D. democraticus*, and the *Scyllinops* complex; and *Acridiophaga caridei*, parasitizing adult *D. maculipennis*, *D. pratensis*, *D. elongatus*, *Schistocerca cancellata*, and the *Scyllinops* complex. The species *P. australis*, and *P. liebermanni* were also occasionally reared from fifth instar nymphs of *D. maculipennis* and *D. pratensis*.

In the field the *Dichroplus* species show a varying susceptibility to attack by the different parasites. Smith (1944) demonstrated considerable physiological resistance on the part of certain Canadian grasshoppers to some sarcophagids and a similar condition is probable within the present South American grasshopper-parasite complex. In this investigation hosts swept together from a given field and caged separately according to species always gave different figures of percentage parasitism by the various sarcophagids. Thus in the vicinity of El Bolson, Argentina, the grasshopper *D. pratensis* is somewhat more abundant than *D. maculipennis*, yet samples of these swept together from mixed infestations showed that the latter species was easily the most favourable host for parasite development. Thus, for example, in the 1949 season early summer samples of *D. maculipennis* bore a parasitism of 2.3%, 1.4%, and 0.5% respectively by *P. liebermanni*, *T. neuquenensis*, and *A. caridei*, whereas the figures for *D. pratensis* were 1.0%, 0.4%, and 0.1% respectively. On the other hand *D. pratensis* and *D. conspersus*, the dominant forms in stations in central Uruguay, appear equally favourable as hosts for *P. australis*. It is not known whether this relative susceptibility is due to the operation of factors acting before or after larviposition by the adult flies.

Biological observations on *P. australis* were made in Uruguay, and those on *P. liebermanni*, *T. neuquenensis*, and *A. caridei* at El Bolson, Argentina. It has been indicated previously that no facilities for temperature control were available, and the subsequent data thus apply under temperature conditions prevailing during the summer at these points.

The four species mate readily shortly after emergence when placed in the sun in small cloth cages, the copulation period varying from 30-120 minutes. Gestation from the time of mating requires between 12 and 16 days. Depending on the species the fully developed first instar larvae lie free in the uteri or are held there still enclosed in the chorions. Larvae deposited on the hosts still within the chorions emerge almost immediately, and it seems more reasonable to recognize this behaviour as larviposition rather than oviposition. The gravid females produce 40 to 80 larvae, except in the case of *A. caridei*, which may develop up to 100. Females swept in the field and later dissected have sometimes been found to contain as many as 20 dead larvae in the uteri, thus further reducing the somewhat low reproductive potential of these species.

The method of larviposition has been observed in the field cages. It is probable that the behaviour of the adult flies towards the grasshopper hosts under these conditions does not depart radically from that of the flies in the

free state. Flies have sometimes been seen to pursue a grasshopper in the field, but it was not possible to identify the species partly on account of the fact that with the low parasite populations occurring in the areas, such incidents could only be observed very infrequently. *P. australis* and *P. liebermanni* patiently "tail" their hosts and eventually deposit the chorion enclosed first instar larvae in the intersegmental folds of the abdomen of the resting grasshopper. *T. neuquenensis* and *A. caridei* deposit naked larvae on the abdomens of the hosts which are approached by more rapid movements than those of the preceding species. This is especially so with *A. caridei*, which has been reported to attack locusts when jumping or in flight in the field, and similar behaviour may be characteristic of *T. neuquenensis*.

The chorion enclosed first instar larvae emerge from the shells within 15 minutes. Penetration of the host by them, and those of species deposited naked, is normally effected through the thinner membranes of the grasshopper abdomen. In all species the larvae lie free in the body cavity and pass through three instars, the mature stage being reached in 15-18 days. The death of the host takes place a few days before emergence of the mature maggots, though occasionally these come out while the grasshopper is still alive. No case of a parasitized individual of *Dichroplus* recovering from attack has been observed, even when only one maggot was present. Feeding in the hosts is usually confined to the wing muscles and fat bodies but the extent to which the host tissues are devoured depends on the parasite species, the number of maggots present, and the sex and species of the grasshopper host. *T. neuquenensis* and *A. caridei* larvae often devour all the internal organs, even those in parts such as the head capsule, so that when they mature the entire host is literally reduced to its exoskeleton. This commonly occurs with small hosts such as the males of various *Dichroplus* species or females of the *Scyllinops* complex, and is not unusual with the larger hosts. On the other hand *P. australis* and *P. liebermanni* larvae at most skeletonize only a part of the host, and as many as ten undersized larvae of the latter species have emerged from a female specimen of the largest solitary grasshopper *D. maculipennis* without producing the completely skeletonized aspect that results from feeding by two or three larvae of *T. neuquenensis*. It is of interest to note that *P. australis* and *P. liebermanni*, two of the most abundant parasites found on solitary grasshoppers, show little tendency to this almost scavengerous habit, while their methods of larviposition also seem better adapted to the nature of the grasshopper hosts. This suggests that they may be the more highly evolved type of grasshopper parasite among the sarcophagids.

The majority of the mature maggots emerge from their hosts through the thin dorsal membranes of the neck, but in all four species under discussion there is some variation in relation to the extent of host feeding. The larvae of *T. neuquenensis* and *A. caridei* in addition to destroying all the internal organs may devour parts of the thin intersegmental membranes of the host's abdominal cuticle, and then emerge at any point in the abdomen including the genito-anal region. A similar abdominal exit occurs much more rarely with *P. australis* and *P. liebermanni*. The number of maggots that develop in each host is variable, being normally one for *A. caridei*, and one to three for *T. neuquenensis*, *P. australis* and *P. liebermanni*. The development of four or five individuals in many *Dichroplus* species is not uncommon, and maxima of ten, seven, and six larvae have been noted for *P. liebermanni*, *T. neuquenensis*, and *P. australis* respectively. Specimens from these larger sized emergences generally transform successfully but it is doubtful if the dwarfed adults reproduce.

Adult life occupies four to five weeks if suitable feeding facilities are provided, and the life cycle from larviposition to adult emergence requires approximately the same period. In the cooler climates such as southwestern Patagonia the four species have one generation and a partial second annually, and as much as 80% of the larvae emerging from the hosts in early summer transform. In warmer areas such as central Uruguay *P. australis* has practically two complete generations, and only a very small percentage of the early summer maggots remain in that stage until the following season. There appear to be no data on the number of generations of *A. caridei* on its normal host *Schistocerca* at these latitudes. Hibernation of the four species occurs as a mature larva in the soil, though *T. neuquenensis* occasionally remains in this stage within the host remains.

The separation of the mature larvae and puparia of the fore-going four species is easily accomplished by examination of a group of characters which include the form of the puparia, the arrangement of the anterior and posterior spiracles, and the extent and pattern of the spinal armature on the floor of the anal pit. These characters are shown in diagrammatic form in Plate 2. Only one specimen (a puparium) of *Opsophyto arteagai* could be obtained for comparison with the above types; its characters were indistinguishable from those of *P. liebermanni*. Distinctions in the shape of the puparia are noticeable particularly in the posterior sections. There is some variation in the number of papillae present in the anterior spiracles. *T. neuquenensis* is typically tripapillate but specimens with two or four papillae are not unusual. Similarly *P. australis* and *P. liebermanni* have anterior spiracles with from five to eight papillae. The posterior spiracles are quite uniform in type. The extent of the spinal armature on the floor of the anal pit varies from a compact, centrally located, two or three rowed group in *P. australis* and *P. liebermanni* to the progressively diffuse arrangements in *T. neuquenensis* and *A. caridei* in which virtually no sections of the pit floors are free from some spine pattern. Smith and Finlayson (1950) have published detailed descriptions of the larvae of some of these species.

Separation of the adult sarcophagids is best done by reference to the original descriptions and diagrams in Blanchard's publications since in the case of such genera as *Protodexia* and *Tephromyiella* the erection of the species is based on small characters of the male genitalia.

Shipments and Exchanges of Parasites

Sarcophagid parasites were dispatched to Canada as mature larvae or occasionally as puparia. Except for a few instances in the 1943-44-45 seasons when rearing was based in Montevideo and Buenos Aires it was found more convenient to hold all parasite material for shipment until the local grasshopper populations had died out at the end of summer (April). Poor communication facilities between outlying localities such as El Bolson, Argentina, and the capital, Buenos Aires, coupled with the need for personal intervention to meet all customs and carrier formalities for the export of shipments, precluded any other arrangements. These formalities had to be completed in the capital cities of Uruguay and Argentina. The loss of some shippable material entailed by this retention was offset by the advantage of forwarding the parasite species in diapause or at least in that stage in which the winter was passed. This increased probability of good survival and at the same time ensured arrival in Canada in a period more suitable for northern hemisphere seasons.

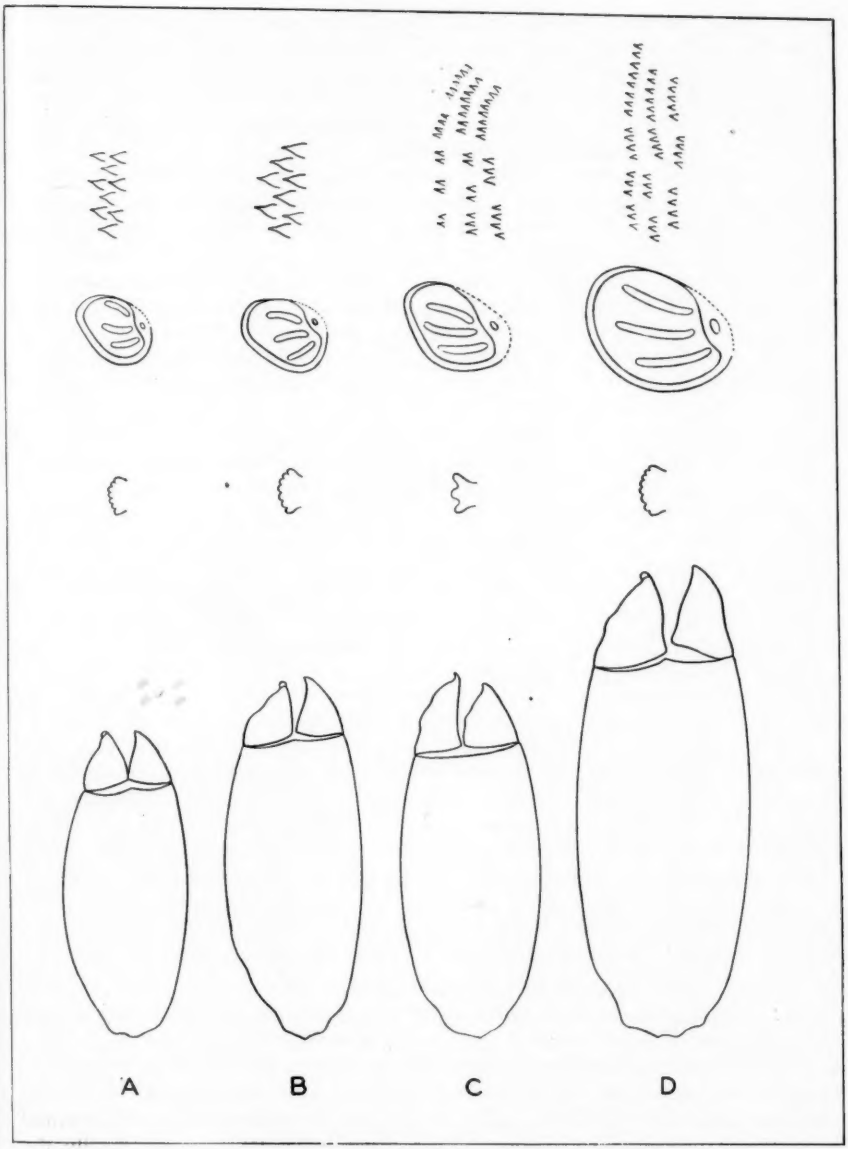

PLATE 2

Diagrammatic representation of puparia, anterior spiracle, posterior spiracle and pattern of spinal armature of (A) *Protodexia australis;* (B) *P. liebermanni;* (C) *Tephromyiella neuquenensis;* (D) *Acridiophaga caridei.*

The method of shipment depended on the parasite stage shipped. With mature larvae up to two hundred of these were placed in damp sand or earth in small salve tins of 2½″ diameter and ½″ depth, and five or six such tins wrapped in cotton wool were then enclosed in 9″ by 5″ by 4″ wooden boxes.

These latter were of strong construction with wood of approximately ½" thickness. The same boxes were used for puparia which were packed in sphagnum moss in a small wire screen cage fastened to one side. Split raisins and cloth pads soaked in concentrated sugar solution were included as food for possible emergents. Each box was sewn in a strong muslin bag prior to dispatch by ordinary air express to Canada.

A total of over eleven thousand mature larvae and puparia of the principal parasite species in Uruguay and Argentina was sent to Canada during the course of the investigation. With the exception of one of the two small shipments of *Acridiophaga caridei*, which had been subjected to excessive low temperatures at the Argentine Laboratorio Central de Acridiologia before being handed over for dispatch to Canada, all shipments arrived in good condition. A small percentage of diseased specimens accounted for most of the mortality.

The investigation by the Dominion Parasite Laboratory, Belleville, of the natural control factors of grasshopper populations in Canada provided opportunity for the collection of numerous parasite species. An exchange of material between the Argentine Ministry and the Belleville Laboratory had been started prior to the writer's arrival in South America. It was understood on both sides that it would be mutually advantageous to continue so doing as part of the general grasshopper project. Unfortunately the Argentine authorities were not in a position to supply any species other than *Acridiophaga caridei*. Although collections involving some thousands of grasshoppers from the Pampa areas of Argentina are usually being handled most seasons by the Laboratorio Central de Acridiologia no material for shipment could be secured because of the lack of field parasitism. The larvae of *Opsophyto arteagai* obtained from *Dichroplus* spp. in the Lamadrid area of Buenos Aires Province during the cooperative work of the 1945-46 season were used for study, and the writer was informed that there have been virtually no recoveries in subsequent years (Salavin 1949).

Four shipments comprising seven hundred larvae and puparia of Canadian grasshopper parasites were received from Belleville for transfer to the Argentine authorities. These species were *Protodexia hunteri* Hough, *Tephromyiella atlanis* Ald., *Sarcophaga reversa* Ald., and *Acridiophaga aculeata* Ald. Although forwarded by air express these shipments were subjected to considerable delays so that practically all material was dead on arrival. A single shipment of 67 *S. reversa* larvae was the only one received in very good condition. The Laboratorio Central de Acridiologia later reported that it had not been possible to build up laboratory stocks from any of these shipments (Oglobin 1949).

Discussion and Conclusions

In reviewing the results of the present survey and comparing them with previous work in other parts of the world, particularly North America, three points call for special mention. These are the relative paucity of the temperate South American parasite fauna of grasshoppers of pest status and its lack of an effective species of practical value in suppressing infestations; the essential similarity of the North and South American parasite complexes; and finally the absence of secondary parasitism.

In Uruguay, Argentina, and Chile definite host relationships are known for eighteen dipterous species of primary parasites and for an uncertain number of mermithids. These diptera include fourteen species of Sarcophagidae, two Tachinidae, and two Nemestrinidae. In the present investigation, restricted mainly to members of the genus *Dichroplus*, eight species of sarcophagids, two nemestrinids, and various mermithids were reared out, whereas Smith (1944) and Buckell and Spencer (1945) recorded at least fourteen primary parasites

of Canadian grasshoppers such as *Melanoplus bivittatus* and *M. mexicanus*. The numerical superiority of the Canadian fauna is due to the presence of four species of tachinids, while only one species from this family is known to attack grasshoppers in temperate South America. This species, *Ceracia subandina* Blnchd., was not recovered in the present survey. It should be noted, however, that although the parasite complex of the Canadian *Melanoplus* grasshoppers would appear to be superior qualitatively to that of *Dichroplus* from South America the over-all parasite fauna of short-horned Acrididae from this area compares favourably in richness with that of North America.

There is no evidence that any of the dipterous parasites found in Uruguay and Argentina are of much value in the reduction of grasshopper populations. Data secured from collections of adult members of the genus *Dichroplus* show that the native parasites do not build up in relatively heavy host infestations, even though they are favoured in at least one respect by the curious absence of secondary parasites such as *Perilampus*. There is some suggestion that these parasites find their most favourable ecological conditions in areas generally characterized by relatively low grasshopper populations such as occur in some valleys of southwestern Patagonia and Chile. These conclusions are supported by the experience of the Argentine entomologists. Even Lahille's enthusiastic opinion of the controlling function of *Acridiophaga caridei* on the locust *Schistocerca cancellata* has received little support from subsequent workers. Although it is recognized that this sarcophagid sometimes effects a very high parasitism in restricted areas, it does not appear to be very effective in the low locust populations, while its powers of distribution are also somewhat unsatisfactory. In this latter respect, the Laboratorio Central de Acridiologia, Argentina, undertook during the *Schistocerca* outbreaks of the past few years, a programme of distributing laboratory reared material to centres of locust infestations where the fly was scarce or absent. This sarcophagid, *A. caridei*, also parasitizes various solitary grasshoppers of the *Dichroplus* and *Scyllinops* groups but observations showed that at least in the more southernly territories of Rio Negro and Chubut it was singularly ineffective and much inferior in abundance to such species as *Protodexia liebermanni* and *Tephromyiella neuquenensis*. The reason for this was not ascertained but was assumed to be related to unsuitable climatic conditions rather than to such factors as host resistance.

The most common sarcophagid species observed in the present collections were *Protodexia australis*, *P. liebermanni*, and *Tephromyiella neuquenensis*, but it was clear from an examination by regular monthly sampling at different stations throughout various seasons that these species played a very small part in the reduction of the local grasshopper populations. Their potential value as parasites for introduction into North America would thus seem low, and it must not be forgotten that these and other South American flies are actually closely related to sarcophagids already known as parasites of grasshoppers on the North American continent. This raises the problem of possible competition for occupation of the same ecological niche. It is particularly interesting to note that, despite the separation by the tropical zone, the broad similarity in the temperate North and South American parasite complexes to which reference was made above does not stop at the level of the families Sarcophagidae, Tachinidae, Nemestrinidae, and Mermithidae but extends down to genera and species. The general *Acridiophaga*, *Protodexia*, *Tephromyiella*, and *Opsophyto*, were erected by Townsend (1933-42) from the types *Sarcophaga aculeata* Ald., *S. hunteri* Hough., *S. atlantis* Ald., and *S. opifera* Coq., and the South American species in these genera are very similar in their system-

atic and biological characters to the North American types. The only known tachinid parasite from southern Argentina is a species of *Ceracia*, and this genus is also represented in the Canadian complex. Finally among the several mermithids present in the River Plate area, the North American *Agamermis decaudata* Cobb, Steiner, Christie, is stated to be common.

In spite of the large numbers of parasites which have been reared from grasshoppers in all parts of the world, few have been considered favourable or promising from the point of view of control. In the latter category have been included species such as *Sarcophaga pachytili* Sk. of Australia, *Wohlfahrtia pachytili* Tns. of South Africa, and *Acridiophaga caridei* Brethes of South America. It would appear from the present investigation that the position in regard to temperate South American grasshopper parasites supports the view put forward by many authors in economic entomological literature throughout the world to the effect that dipterous and other parasites are of little value in the control of such pests.

Summary

In connection with a study of the natural control of grasshoppers in Canada a survey was made for exotic species of parasites in that part of temperate South America comprised by Uruguay and Argentina.

Rearing was done at various centres by the use of a number of collapsible cages which permitted handling up to 25,000 adult grasshoppers at any one time.

Details are given of the grasshoppers and locusts of pest status in these countries and their recorded parasites. Samples of 320,000 *Dichroplus* hosts and approximately 40,000 members of the *Scyllinops* complex were examined from various localities in Uruguay and Argentina during the period 1943-49 and two tables showing the parasitism by diptera at 24 sampling stations are given. This parasitism was based on an estimated emergence of two larvae per host, an estimate probably giving somewhat liberal figures since from one to ten larvae of the various sarcophagids can successfully develop in the hosts. The maximum percentage parasitism by diptera of any seasonal sample from a station was 8.1 and most figures were well below that. Smaller collections were sometimes parasitized up to 25%. A parasitism of 20% by unidentified mermithids was noted in two small samples of *Dichroplus* species taken at the end of the season from parts of central Uruguay. In areas fringing the Argentine southern Andes where there remain tracts of primitive vegetation the dipterous parasitism was better both qualitatively and quantitatively than that in the more open pampa type of habitat.

Eight species of sarcophagids, two nemestrinids, and several unidentified mermithids were reared out. The parasites encountered were the sarcophagids *Protodexia australis* Blnchd., *P. aleuaphaga* Blnchd., *P. liebermanni* Blnchd., *Tephromyiella neuquenensis* Blnchd., *Acridiophaga caridei* Brethes, *Opsophyto arteagai* Blnchd., *Hypopelta salavini* Blnchd., and sp. Y; the nemestrinids *Neorhychocephalus sulphureus* Wied., and *N. vitripennis* Wied. The complex of parasites at the different stations is given. The species *P. australis* and *P. liebermanni* were generally dominant but the *Neorhyncocephalus* and mermithids were more abundant in certain localities.

Biological data are included on the four most important sarcophagid parasites, namely *P. australis*, *P. liebermanni*, *T. neuquenensis*, and *A. caridei*.

The general paucity of the temperate South American grasshopper parasite fauna with its lack of effective species of practical value, the broad similarity of the parasite complexes in North and South America, and the curious absence of secondary parasitism in South America, are discussed.

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The Time Factor in Biological Control

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The Presidential Address given by C. P. Clausen to the 62nd Annual Meeting of the Association of Economic Entomologists and recently published in the Journal of Economic Entomology (1) contains much food for thought for workers in the field of biological control. The thesis developed by Clausen in his address is, briefly, that any introduced parasite or predator that is destined to produce full commercial control will do so within three generations or at most within three years. If it does not produce full commercial control within this period it is safe to say that it will never do so. Species that prove ineffective after three generations or three years from the period of introduction should therefore be dropped and efforts directed toward the introduction of other species.

If we accept this principle and apply it as it stands to biological control work we must I think write off a very great many of the practical experiments that have been made as failures. We may have thought on the basis of certain arguments that with the course of time, introductions that have not yet given conclusive results, will eventually turn out to be of great value; but if Clausen's arguments are valid these expectations are illusory.

Clausen's views have not been hastily formulated. He has held them for at least a decade. Since he has made them the subject of his Presidential Address to the Association of Economic Entomologists we may take it that they represent his settled conviction. Clausen himself is a worker whose practical accomplishments and scientific writings command general respect. The views he has expressed therefore deserve careful examination.

Though the statement given above represents what we believe to be the essential features of Clausen's view it is accompanied by certain qualifications and restrictions which a fair presentation must include.

In the first place Clausen limits his discussion to parasites and predators that consistently exercise what is termed full commercial control of the host. *Full commercial control* is defined by Clausen as that degree of control beyond which other methods of control are not required or are economically impracticable. A parasite or predator is defined by Clausen as *effective* when it consistently holds its host under full commercial control year after year irrespective of influences that may tend to cause the populations of the host to oscillate widely. Such parasites and predators are affected by environmental conditions *in the same way as their hosts.* By this we mean that any conditions favouring the increase of the host will also favour the increase of the parasite. This evidently does not mean simply that factors producing an increase in the host populations would favour the parasite through an increase in host density but rather implies that all environmental factors favouring the host will be equally favourable to the parasites.

If a parasite or predator exercises commercial control and even complete commercial control, *from time to time*, reverting in the intervals to a state of

ineffectiveness Clausen considers it to be an ineffective or partially effective parasite. In the case of such a parasite the variation in environmental conditions is not always favourable to it when it is favourable to the host and this is what reduces the parasite to a state of ineffectiveness.

Clausen considers that an effective parasite will produce control in three generations or at most in three years. He does not claim in this short period complete commercial control will be achieved over the whole area of infestation. He considers however that in this time effective commercial control will be produced in the area over which the adult of the first field generation will spread from the colony site. In some slow moving species this area will of course be small and may be limited to a few acres. In large and active species, such as some of the Tachinids the area of spread might be several square miles. Nevertheless whether it is small or large an effective parasite may be expected to control the host commercially over this area within three generations or three years at most. Clausen would expect to obtain this effect even if there is only a single generation per annum.

Clausen points out that several authors have presented detailed mathematical computations based mainly on the relative reproductive potential and length of life cycles of host and parasite to show that the latter is able to overcome its host only after a long time interval. He cites L. O. Howard as maintaining that a rather prolonged period of time will be required to enable the parasite to catch up with the host owing to the initial discrepancy in numbers since in actual practice the number of parasites liberated in the colony is usually quite small, while the number of hosts in the area is usually enormous. However, Clausen considers that the reasoning of the authors he refers to is contradicted by the facts. His own thesis is based, not on mathematical theory or numerical calculations but on the observed results of field experiments and these he claims show nothing to substantiate the belief that a parasite may remain ineffective during a long period and yet eventually achieve the point where it is able to produce commercial control.

Some workers entertain the belief that a parasite may be ineffective in a new environment for a considerable time not so much because its population is small as because it is imperfectly adapted to the environment in the area. They believe that it may then become adapted to local conditions after which it will produce satisfactory control of the pest against which it has been introduced. Clausen rejects this idea. Not one instance, he says, can be cited to support the belief that an introduced parasite will adapt itself to a new environment and eventually become more effective than in the years immediately following its importation.

The final important point concerns the establishment of parasites and predators. If the parasite or predator has been liberated in adequate numbers in all the different climatic areas inhabited by the pest at a time when the host is at the right stage for attack it will, if it is of any value, become established immediately. If, though the numbers liberated are adequate and the host is in the right stage, difficulty in establishing it is experienced we may conclude that it will never produce complete commercial control. Rapid establishment is of course not a guarantee that complete commercial control will eventually be obtained but difficulty in establishment practically guarantees that it will not occur. Clausen's thesis on the rapidity of control by effective parasites is not as we have already said, a deduction from theoretical considerations but an induction from field observations. He gives a list of 15 or 16 species in which the course of events was in conformity with his views. He is careful to point out that rapid initial control does not necessarily imply permanent control and mentions some instances

in which introduced species have been very effective for a short period but have afterwards declined. In further support of his view Clausen mentions the very rapid increase and spread of pest species such as the Japanese beetle and indigenous parasites such as the Braconid Aphidius on the Green Bug and other Aphids. Finally he points out that those who believe that effective control can be obtained with an introduced parasite or predator after a long period of ineffectiveness are unable to adduce any positive evidence from field observations in favour of their contention.

Clausen's argument though brief is certainly impressive and stimulating. The present writer has devoted a good deal of attention to the mathematical theory of biological control but has been careful to point out that we cannot depend on mathematical theory to tell us what happens in nature. For this we must rely on experiment and observation. Mathematical computations which are of the type mentioned by Clausen and are perhaps those he had specifically in mind were made by the writer in papers published from 1922 onwards (2). He would not maintain that these computations have the same status as field observations.

However, when we are presented with a generalization concerning a succession of quantitative values, even as an induction from field experiments, we still feel that we should like to develop it deductively from mathematical premises. The hypothesis constituted by these premises may not correspond to the facts. Nevertheless, in so far as it produces the numerical sequence that occurs in Nature, it makes the origin of this sequence intelligible, though it remains factually uncertain. It therefore seems interesting to enquire how Clausen's hypothesis can be mathematically justified.

It should be pointed out that the generalized mathematical expression developed by the present writer in the articles referred to above does not produce as a necessary mathematical consequence the conclusion that the populations of introduced parasites develop very slowly and produce economic control only after a long period of generations. This is simply *one* result one obtains by giving certain values to the variable in the formula. If other values are given the results obtained are perfectly consonant with the views of Clausen. In fact they explain certain aspects of his general thesis that seem at first sight to be rather paradoxical, in a surprisingly simple and satisfactory manner.

No reader of Clausen's article can help remarking his firm and frequent references to the figure of three generations (or at most three years) as the time required for a really efficient parasite to effect commercial control, as contrasted with the vague and indefinite description of the other conditions or factors which have to be taken into account. Thus Clausen says that the colony of parasites must be *adequate* but he does not define what he means by this word. He states that an effective parasite will produce control in a period of three generations or three years in the area to which the first field generation has spread. Nevertheless he clearly recognizes the fact that owing to differences in mobility the area covered by the first field generation of one species might be very small amounting only to an acre or less, while the area of distribution of the first field generation of other species might be extensive, amounting to several square miles. It is clear, other things being equal, that in the first case we might have a very high ratio of parasites to hosts whereas in the second case the ratio of parasites to hosts would be very low. At first glance it would seem that a parasite population spread very thinly over a very large host population could hardly effect control in anything like the same time as when it is concentrated in the midst of a much smaller host population. Furthermore the rather

casual way in which Clausen passes from the figure of three generations to the figure of three years, in which a considerable number of generations might occur, is, at first sight rather confusing. It almost suggests that for Clausen the number three has some special and almost magical significance.

However when the problem is examined from a mathematical standpoint these difficulties largely disappear. In order to simplify the discussion let us say that the host population has ceased to increase and that complete commercial control is obtained when the parasite population becomes equal to the host population. Let the host population be represented by n, the parasite population by p, the reproductive rate of the parasite per generation by s and the number of generations by t. Control will thus occur when we have

$$n = ps^t$$

This equation by a simple transformation becomes

$$t = \frac{\log n/p}{\log s}$$

Now putting $s = 10$ and $p = 10$ consider the value of t obtained with different values of n. As a simple calculation will show, when $n = 100$, $t = 1$; when $n = 1000$, $t = 2$; when $n = 10{,}000$, $t = 3$ and when $n = 10{,}000{,}000$, $t = 6$. Thus if the host is ten times as numerous as the parasite, the parasite will effect complete control in one generation; if it is 100 times as numerous, in two generations; if it is 1,000 times as numerous, in 3 generations and if it is 1,000,000 times as numerous, in 6 generations. Thus the apparently narrow margin that Clausen allows himself between three generations or three years is in fact amply sufficient to take care of the differences in the ratio of host and parasite populations that would result from the differences in spread that he mentions. Furthermore it is clear that for the same reason he is under no particular obligation to give an exact value to the "adequate" colony. It is in fact clear that the size of initial colonies might differ very considerably without causing the time required for commercial control to fall outside the limits which Clausen has set for himself.

If a parasite or predator is really adapted to the environment into which we introduce it, its effective reproductive rate will tend to approach its potential reproductive rate. As is well known the potential reproductive rate of insects is very high. Even a small initial parasite population increasing generation by generation at anything near its potential reproductive rate could easily rise within the time specified by Clausen to astronomical figures allowing it to cope with any ordinary infestation of a pest which was not itself increasing in numbers.

These curious and rather surprising consequences follow of course from the simple fact that we are dealing with geometrical progression or in other words with the growth of something whose rate of increase is proportional to its dimensions at that moment. This is a case in which mathematical theory and reality coincide for all practical purposes. It is rather like the mathematical relations within a real sphere as compared to those in the ideal mathematical sphere. We shall not expect to demonstrate in the real sphere the precise relation between radius and surface that we can demonstrate in the ideal sphere but it will be near enough for practical purposes. The parasite population in the field will not increase generation by generation at exactly the same rate; but we can be sure that the increase will have the general characteristics of an increase by geometrical progression. The importance of this matter was brought out by the present writer in a paper published in 1927 (3) outlining a method for the approximate calculation of the progress of introduced parasites of insect pests. The foregoing remarks simply exemplify the calculations given in that paper.

The assertion of Clausen, that a parasite which reveals itself during the first few years after establishment, as an inefficient control of the pest against which it has been introduced, will not adapt itself to the environment so that it becomes an efficient parasite, cannot be tested mathematically. It seems, however, to be in conformity with the known facts. It would be easy to cite parasite species which have continued for as long as we have been able to observe them, at a very low numerical level, not only in areas into which they have been artificially introduced but also in the country of origin. If rapid adaptations frequently occurred, transforming a very poor controlling agent into a good controlling agent, they would by now have been noticed by students of natural control. In fact the limitation of adaptiveness that Clausen notes in parasites is simply a special case of the general limitation in adaptiveness that we observe in all animal and plant species. We know of cases where an organism flourishes better after migrating to a distant area than it has in the original home, but this appears to be due to the fact that its requirements happen to be better satisfied by conditions in the new environment: not by a genuine adaptation.

The fact that parasites or predators, though potentially capable of flooding the environment, merely continue to subsist for long periods at a low numerical level, demonstrates that the multiplication and spread that they exhibit, when introduced into new areas, is not necessarily the prelude to effective action as controlling agents; but rather an episode of brief duration after which the population becomes more or less stabilized and never makes any notable advance.

Furthermore, we may expect that a parasite or predator that is really efficient in Clausen's sense, will be a rarity. It is easy to see that as we pass along the chain that leads from the physical environment to the entomophagous parasite, the difficulties of existence increase. Plants, though sometimes closely restricted in habitat, have, in general a wide distribution. Phytophagous insects, to subsist, must find their host plants. The practice of rotation often complicates this process for insects feeding on agricultural crops. Finally, the entomophagous parasites must locate in the relatively enormous area into which, they emerge, their widely scattered mates and insect hosts. The more specific the parasite is in its choice of hosts, the greater its difficulties will be, other things being equal.

The qualities a parasite must possess, to be an efficient controlling agent in Clausen's sense, constitute a combination not easily realized. The parasite must be extremely specific in its choice of hosts, otherwise it will use its killing power against hosts other than the one we wish it to control. With this specificity there must go an exceptional faculty to locate the host and to attack it effectively: so that neither low host density nor development in micro-habitats that would protect against less efficient species, seriously impede it. Furthermore, its reactions must be such that any conditions favorable to the host insect, favor it also; while conditions unfavorable to the host must not depress it sufficiently to allow a host outbreak. Thus, in its host relations, the parasite must be highly specialized, while in its relations with the environment in general it must not be highly specialized but able to flourish under a variety of conditions. These characteristics are more frequently found separately than in combination. We can think of Tachinids like *Winthemia quadripustulata* F. or *Exorista larvarum* L. which are clearly very catholic in their choice of environments but never seem to be very important as controlling agents; we know others, like *Fortisia foeda* Mg., the parasite of *Lithobius* or the *Melanophorine* parasites of woodlice, which are extremely specific in their choice of hosts, but, as controls of these hosts, are negligible factors. But the combination of high specificity and high efficiency is much less common.

The available evidence therefore suggests that in many cases the introduction of entomophagous insects into a new area may be followed by an increase and spread continuing for a considerable time without ever bringing the species concerned to the point where they are effective controls in the sense of Clausen. The unsatisfactory character of the parasite will naturally exhibit itself in a low reproductive rate; this low reproductive rate will prolong the period that precedes stabilization. On general grounds, therefore, we may expect many if not most of our introduced parasites to increase slowly to the point where they take a more or less fixed but relatively unimportant toll of the host population but never succeed in controlling it permanently and commercially.

Clausen maintains that difficulty in establishing an introduced parasite is a reliable indication that it will never be effective. However, he adds the proviso that the rule holds only if the species has been released in "adequate" numbers. Since "adequate" can hardly mean anything but adequate for establishment the rule can apply only in cases where establishment depends on numbers. Clausen says also that the liberation tests must cover all the different climatic areas inhabited by the host; and that adequate recovery work must have been carried out. Most workers in biological control would agree that there is little justification for continuing to turn out large numbers of a parasite which has already been distributed in hundreds of thousands during a period of years over a wide area.

But when all these concessions have been made, we have not yet reached the point where we can see any rational justification for Clausen's main thesis: that a parasite which cannot achieve commercial control of the host in a matter of three years, will never achieve it; or, to put it in another way, a parasite that is still at a low numerical level with respect to the host, at the end of three years, in the area to which the first generation has spread, will never rise to the point where it holds the host population permanently below the level of economic damage.

As we have already said, the mathematical formulation of the problem given above, though it seems inherently plausible, does not necessarily lead to the conclusion that a parasite population will develop slowly over a long period and yet eventually rise to the point where it produces economic control. However, this is certainly *one* of the possibilities represented by the formula. If the rate of multiplication of the parasite is not very high and the initial population of parasites is small, in relation to the host population, then it will take a much longer time than Clausen allows, for the parasites to overtake the hosts. For example, if the host is 1,000,000 times as numerous as the parasite, and the latter increases 10-fold per generation, it will come to equal the host in 6 generations; but if its reproductive rate is only 2-fold, this will require 20 generations; if it is only 1½-fold, 34 generations.

Considering the potential reproductive rate of most parasites, which may easily be 100-fold, it seems that a parasite with only a 2-fold increase per generation must be classed as inefficient. But this does not mean that it will not eventually bring the host under control. It may fail to do so because it cannot maintain its geometric progression; but this failure may be quite unrelated to the fact that the effective reproductive rate is normally low. Thus, if a proportion of the hosts is inaccessible in every generation, a parasite might have a high reproductive rate while plenty of accessible hosts were available; but the rate will fall eventually in much the same way as it does on the Vebrulst-Pearl hypothesis.(4)

When the initial parasite population is small in comparison with the host populations and the effective reproductive rate not very high, the percentage of hosts parasitized will remain low for a considerable period, rising abruptly toward the end of the parasitic cycle. Thus, if n—10.000, p—10 and $\frac{s}{h} = 1.5$, the percentage of parasites in the successive generations will be as follows:

t	1	2	3	4	5	6	7	8
%	0.15	0.225	0.33	0.508	0.766	1.16	1.76	2.70
t	9	10	11	12	13	14	15	
%	4.15	6.50	9.6	18.6	34.2	78.0	100%	

But this expresses the relation of the *total* populations of host and parasite. In fact, as the present author pointed out in one of his first articles on this subject (1922) there may be local concentrations of the parasite and thus in certain spots, a very high parasitism. Indeed, this seems more likely than an even diffusion of the parasite population throughout the entire host population.

A theoretical treatment of this problem is not easy to produce. It may be simplified if we would postulate that the host population is uniformly distributed and then suppose that the parasite population spreads backward and forward from a point on a base line, migrating in each generation a definite distance perpendicular to this line.

It is immediately clear that on such postulates, the outer limit of the parasite population will move farther and farther from the base line extending by one flight distance in each direction in each generation.

But this will not result in a uniform distribution of the parasite population. Suppose we have an initial population of one parasite with an effective reproductive rate of 2. The 2, F1 progeny will be on the +1 and —1 flight lines. In the F2 generation, however, 1 will move to +2, 1 to —2 and 2 to the base line. In F2, therefore 50% of the progeny will be back on the base line. In F3, there will be 3 parasites on the +1 flight line, 3 on the —1 flight line, 1 on the +3 flight line and 1 on the—3 flight line. Thus, 75% of the parasite population is still 1 flight distance from the base line. In F4, the 16 individuals in the parasite population are distributed as follows: 6, or 37% on the base line, 8 or 50% on the second flight lines, 2 or 12.5% on the 4th flight lines. Thus 87% are on or within the 2nd flight lines. In F5, of the 32 individuals, 20 or 62.5% are on the first flight lines, 10 or 31% are on the 3rd flight lines and 2, or 6.2% on the 5th flight lines. In F6, we have 64 individuals. Of these, 20 or 31% are on the base line, 3 or 47% on the 2nd flight lines, 12 or 18.7% on the 4th flight lines and 2 or 3.1% on the 6th flight lines. Thus, even in F6, 78% of the population are still on or within the 2nd flight lines. In F7, we have a population of 128 parasites, distributed on the 1st, 3rd, 5th and 7th flight lines but 112 or 87.5% are on, or within the 3rd flight lines.

Thus, on the postulates adopted, the concentration near the base line remains for a considerable period, much greater than one might expect. When a small colony of parasites is placed in the midst of a large host population spread over a wide area, one naturally expects that collections in the vicinity of the colony will show a much higher percentage of parasitism than the percentage obtained by relating the total host population to the total parasite population because the parasites, having limited powers of dispersion will not distribute themselves with mathematical uniformity with respect to their hosts. Nevertheless on the postulates adopted above, the distribution of the parasites is much less uniform than might be anticipated with respect to the host population, even within the limits of their dispersion. In F7, the 14 flight lines and the base line, in a uniform

distribution, would carry about 8 parasites each, so that 37% would be beyond the 3rd flight line; whereas only 12.5% are beyond it.

The point we are trying to make here, is that, on theoretical grounds not devoid of plausibility, we may surmise that the routine collections made after the liberation of a parasite colony, will show a much higher degree of control than is given by mathematical formulae which relate the total population of the parasite to the total population of the host. If, even in the area of parasite distribution, the parasitism remains low, then we may suspect that the parasite is an inefficient species and will never exercise commercial control. On the other hand, even a high local and temporary parasitism is no guarantee of permanent control over the whole of the infested area.

The foregoing considerations, taken together, go some way to justify the theses advanced by Clausen. This justification consists in the fact that if entomophagous insects behave in the manner described by certain mathematical hypotheses, we can deduce that the sequence of events will be as Clausen describes it. The efficient parasite will bring its host under control in a short time, in the area over which the first few generations have dispersed. If it does not do this, the chances that it will ever be an effective control, are small. There is little hope that a low percentage of parasitism over a long period, is the prelude to a rise to the point of effective control.

On the other hand, the difference between the views of Clausen, based on empirical evidence and those expressed in connection with the mathematical computations to which he refers, is perhaps less striking than he supposes. If, in the case of a really efficient parasite producing local control in a few generations, the percentage of parasitism in the succession of generations, is calculated by relating the total parasite population to the total host population, the curve might closely resemble that in the table given (p. 236). Clausen indeed appears to envisage this possibility since he allows that the control effected in the space of 3 generations may relate only to an extremely small fraction of the total infested area; from which it follows that complete control over this area may take a good many years.

We must point out, once more, that the view criticized by Clausen was expressed with qualifications he has not mentioned. In proof of this the writer may quote from one of his own papers published on the mathematical theory of biological control some 30 years ago (1).

In this paper, utilizing the formula for percentage of parasitism developed in a previous communication, some numerical examples were worked out. From these some general conclusions were drawn.

"These examples", it was said, "show that, in all the cases considered, the general form of the curve of parasitism is the same. This curve rises very little for a considerable time for any increase in the value of t (number of generations) but towards its end, on the contrary, it rises more and more rapidly."

"The greater the initial proportion of hosts, the more the first part of the curve is prolonged, the terminal part retaining approximately the same form."

"If the reproductive power of the parasite is greater than that of the host, an increase, even considerable, in the initial number of hosts, that is to say, in the value of n (hosts) in relation to p (parasites) determines only a relatively feeble prolongation of the initial portion of the curve. The greater the reproductive power of the parasite in relation to that of the host, the less an increase in the value of n will affect the initial part of the curve."

"If the reproductive power of the parasite is only equal to that of the host, a relatively feeble increase in the value of n will produce a considerable elon-

gation of the initial portion of the curve, that is to say, of the part which corresponds to the low values of *a* (percentage of parasitism)."

"We may therefore conclude, other things being equal, that if we introduce a colony of parasites in a large population of hosts, the effect of this introduction may be scarcely perceptible for a very long time; and that, not merely to the ordinary observer, but to the trained entomologist, because, in certain cases, the percentage of parasites rises very little in a generation especially if the number of hosts is very large in relation to the number of parasites and the reproductive power of the parasite is only equal to that of the host".

"If the parasite disperses very slowly from the colony site and if, to calculate the increase of parasitism per generation, we study only collections made in this region, we shall obtain figures that are much too large in relation to the totality of the infested area; but if the parasites disperse rapidly, our figures are more likely to be valid."

In the next paragraph of this article it is said that on the hypotheses adopted, it would require 19 generations for a colony of 1000 parasites to overtake and exterminate one thousand million hosts, when the reproductive rate of the parasite is twice that of the host; and during the first 16 generations, the percentage of parasitism, in the infested area, considered as a whole, would not attain 10%.

But, it was pointed out, there may be, during this long period, local concentrations of the parasite, followed by disappearances, owing to the action of purely temporary factors. There may be, in a given generation, restricted areas that are overpopulated, and nearby, other localities where the parasite is very scarce. At one point, the parasite may exterminate a small colony of the host; in another the host may be practically free from attack.

It seems therefore, that if we put side by side the theses of Mr. Clausen and the present writer, with the qualifications and reservations attached by both, they do not notably differ; and the writer believes that this would apply to other workers, like the late Dr. L. O. Howard, who have used mathematical computations in discussing the theory of biological control.

However, the empirical evidence assembled by Clausen suggests that sufficient weight was perhaps not given to the possibility that the sequence of events in the vicinity of a colony site, during the first few years after the liberation of an introduced parasite or predator, is an *index* to its value as a controlling agent over the whole area of infestation or over a great part of it. If the spread of a parasite normally takes place in the manner postulated above, then the phenomena around the colony site will constitute in some sense, a replica in miniature of what we shall eventually see in the whole of the infested area; and the observation of this limited zone will enable us to predict with reasonable accuracy, what will eventually occur over hundreds or thousands of square miles.

Most workers in biological control, I believe, have usually felt that rapid establishment and increase in the vicinity of the colony site is an encouraging phenomenon but they have perhaps been too reluctant to admit that difficulty in establishment and a low reproductive rate in the field, in the vicinity of colony sites, is a real indication of permanent inefficiency. They have been inclined to think that the phenomena around the colony site are a replica, not of what will eventually happen in the whole area, but of what is *actually* happening there and have hoped that although the observable increase in parasitism is slight or indeed almost undetectable for a considerable period the characteristic rise will eventually occur. On the basis of such vaguely optimistic views, the introduction, mass breeding and distribution of certain parasites and predators

has sometimes been continued for years, even in the absence of any encouraging evidence from field studies.

As we have already said, the arguments that can be advanced in favor of Mr. Clausen's theses are not completely convincing. The empirical evidence produced, though impressive, is lacking in precision. It does not appear to *explain* the events that have been observed to occur. We have endeavoured to make good this defect by the use of the hypothetico-deductive method, showing that from certain fairly reasonable postulates the theses of Clausen can be deduced as a possible consequence.

It must however be said, on the one hand, that the factual basis of Clausen's contentions is rather inadequate and, on the other, that to show how things could happen in a certain way, is not a proof that they did happen in that way. The hypothetico-deductive method, in spite of its great successes in certain fields of science, is not, as some think, the only, nor even the best way of discovering the truth about nature. It is not a substitute for direct observation; and it is precisely the woefully inadequate character of our information on the increase and spread of introduced parasites that makes it so difficult at present to test any of our hypotheses in regard to biological control. The energy expended in the introduction, mass breeding and distribution of parasites has been and still is quite out of proportion to that expended on efforts to find out and understand, what happens in the field. It is only by the careful and continuous study of the increase and dispersion of introduced parasites and the exact evaluation of their importance as controlling factors that biological control can rise above the crude empiricism of its present status.

Dr. Clausen's theory may perhaps be criticised as one-sided. His practical objective is the discovery of a species of parasite or predator capable by itself of effecting complete commercial control within a short period of time. The idea that by the accumulation of a number of species attacking different stages or attacking the same stage in different micro-environments, a controlling complex might eventually be built up, is not clearly envisaged by him. Yet when we consider the natural control of organism in the native environment, we are almost always forced to ascribe the limitation of their numbers to a combination of factors, biotic and physical, varying from time to time and from point to point. Rarely do we find cases in which a species is held down to a low numerical level by a single parasite or predator. Even when a particular species has given outstanding results after introduction into a new area, it was not always possible to predict this by considering its behaviour in the country of origin. The Coccinellid *Cryptognatha nodiceps* gave spectacular control of the Coconut Scale, *Aspidiotus destructor* in Fiji; but it does not stand out among the natural enemies of this pest in the West Indies. The Galerucid Beetle, *Schematiza cordiae*, shipped by the Commonwealth Institute of Biological Control to Mauritius for the control of the weed, *Cordia macrostachya*, gave outstanding results, so that the experiment may be ranked among the major successes in the biological control of weeds. But the careful investigations of *Cordia* insects made by F. J. Simmonds did not enable him to predict this success.

Nevertheless, in spite of any reservations or criticisms we may feel inclined to make, the views advanced by Clausen in his Presidential Address to the Association of Economic Entomologists are a challenge to all workers in the field of biological control: a working hypothesis which it is imperative to test, since it may eventually form the basis of a drastic and thorough-going revision of our practical programmes and our plans for research.

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Mass Flights of the Spruce Budworm[1]

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During the course of an investigation of the dispersal of the spruce budworm[3] (Henson, 1950), mass flights of the insect have been studied. The records of these flights are to be found in the files of the Forest Insect Laboratory, Sault Ste. Marie, Ontario, but in many cases these records are not complete. Nineteen flights for which sufficient data exist have been examined.

Certain characteristics of the flights are quite constant and may be interpreted in the light of our present knowledge of the insect. The mass flights always take place in the evening or early part of the night. The farther the area of deposition from an infestation, the later at night the flight is observed. In all cases, a cold frontal passage followed the deposition of the insects. In some cases, rain preceded the flight of the insects, but the period of rainfall was usually brief.

From the times at which the flights have been observed, it is evident that the moths become airborne during the early evening. The normal daily flight of the insect begins during this period. It has been shown (Henson, 1950) that the heavy evening flight of the moths is a response to light of decreasing intensity, the numbers of insects in flight being directly related to the rate of decrease of light. Reconstruction of the meteorological situations at the times of the mass flights leads to the conclusion that the insects were carried by convective storms which precede typical cold fronts.

Sudden thunderstorms that cause a sudden reduction in the amount of light and also bring about pressure changes are known to result in heavy flights of moths. It is felt that the prefrontal thunderstorms are responsible for the initiation of the mass flights.

In the structure of a typical thunderstorm, there is a strong updraft in the front of each cell of the storm. This updraft is often observed from the ground as the wind which blows towards the approaching storm. Insects in flight when this updraft passes over an area may be drawn up into the storm. The high speeds and persistent nature of the updrafts in a convective storm may result in the transportation of insects to considerable heights. Insects drawn up into a thunderstorm might be tossed out the sides or top of the cloud, deposited with the rain in the central downdraft, or carried in the storm.

The physical conditions inside a thunderstorm which moths would have to endure are not necessarily fatal unless the insects are carried to that part of the storm where they would be coated with a layer of ice (Wellington, 1945). From all accounts, insects which are deposited after a mass flight are battered but still quite active.

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[3]*Choristoneura fumiferana* (Clem.)

An Annotated List of Lepidopterous Larvae from Commercial Blueberry Fields, Charlotte County, N.B.[1]

By G. W. Wood[2]
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A comprehensive study of insects affecting the low-bush blueberry in New Brunswick was begun in 1946 largely because of the destructive outbreak of *Actebia fennica* (Tausch.) in 1944 and 1945. The work was carried on in Charlotte County, where most of the commercial blueberry areas of the Province are located. This paper deals only with the lepidopterous larvae, among which are found the most important pests, such as climbing cutworms, loopers, and leaf tiers.

The species listed were collected principally by sweeping the blueberry fields at night with a stout insect net. A few species were taken by day sweeping and hand picking. Collections were made from representative fields in all parts of the County. The number of larvae collected by making 50 sweeps with the sweeping net was established as a standard sample. All larvae were brought into the insectary and reared individually in jelly jars, fresh blueberry foliage being supplied daily. The notes on life-history and parasitism were recorded from insectary-reared specimens. Light and bait traps were used to obtain data on flight periods and oviposition.

Much helpful advice was obtained from Mr. C. W. Maxwell, Officer-in-Charge, Fruit Insect Laboratory, Fredericton, N.B., under whose direction the work was carried out.

Determinations were made by officers of Systematic Entomology, Division of Entomology, Ottawa, as follows: Lepidoptera, Dr. T. N. Freeman, D. F. Hardwick, and Dr. E. G. Munroe; Braconidae, G. S. Walley and W. R. M. Mason; Chalcidoidae, Dr. O. Peck; Ichneumonidae, G. S. Walley; and Diptera, G. E. Shewell.

List of Species[3]

Phalaenidae

1. *Actebia fennica* Tausch.

Present in outbreak numbers in '44 and '45. Collected in '46, '47, '48, '49, and '50 in May and June, pupated from June 9 to July 13, and adults emerged from July 1 to Aug. 5. Light-trap collections indicate that adults are in flight until the first week of September. Parasites reared were *Arenetra canadensis* Cress. and *Poecilanthrax tegminipennis* (Say).

2. *Rhynchagrotis cupida* Grt.

Collected in '48, '49, and '50 in May, pupated from June 11 to July 17, and adults emerged from July 13 to Aug. 14. Parasites reared were *Apanteles* sp.

3. *Protolampra rufipectus* Morr.

Collected in '48 and '50 in May and early June, pupated from June 28 to July 16, and adults emerged from Aug. 1 to Aug. 30.

4. *Graphiphora smithi* Snell.

Collected in '47 and '50 in May and early June, pupated from June 16 to July 30, and adults emerged from July 30 to Aug. 26. Eggs laid in late August and early September, and hatched within a week. Commonly taken by light trap. Parasites reared were *Zele crassicalcarata* Vier. and *Copidosoma* sp.

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[3]Brackets have been purposely omitted in scientific names of lepidopterous species in this paper.

5. *Graphiphora collaris* G. & R.

Collected in '47, '49, and '50 in May and early June, pupated from June 13 to July 30, and adults emerged from Aug. 20 to Sept. 9. Eggs laid about the first of September, and hatched in 10-11 days. Commonly taken by light trap. Parasites reared were *Ophion* sp. and *Rogas* sp.

6. *Euxoa perpolita* Morr.

Collected in '49 and '50 in May and June, pupated from July 24 to Aug. 29, and adults emerged from Aug. 12 to Sept. 30. Commonly taken in light and bait traps.

7. *Euxoa declarata* Wlk.

Collected in '47, '49, and '50 in May and June, pupated from July 20 to Sept. 13, and adults emerged from Aug. 10 to Oct. 30. Commonly taken in light and bait traps.

8. *Eurois occulta* Linn.

Collected in '48 in May, pupated from June 3 to June 6, and adults emerged on July 3 and July 4.

9. *Feltia ducens* Wlk.

Collected in '48 and '50 in May and June, pupated from July 30 to Aug. 14, and adults emerged from Sept. 1 to Sept. 14. Commonly taken by light trap. The parasite *Chelonus* sp. near *sericeus* Say was reared from this species.

10. *Spaelotis clandestina* Harr.

Collected in '47, '48, '49, and '50 in May and June, pupated from May 30 to July 8, and adults emerged from July 2 to Aug. 4. Mating and oviposition from late August to early September; eggs hatched in October and November. Rarely taken by light trap. Parasites reared were *Pterocormus rufiventris* (Brullé), *Microplitis* sp. near *autographae* Mues., and *Apanteles laeviceps* Ashm.

11. *Agrotis mollis* Wlk.

Collected in '47 in May, pupated in early June, and adults emerged on June 28. Adults have been collected throughout July by light trap.

12. *Polia purpurissata* Grt.

Collected in '47, '48, '49, and '50 in May and early June, pupated from June 6 to July 10, and adults emerged from July 7 to Aug. 29. Eggs laid in August, and hatched within 10-11 days. Commonly taken in light and bait traps. Parasites reared were *Ophion* sp., *Erigorgus* sp., *Therion* sp., *Eulophus* sp.?, and *Coelopisthia* sp.

13. *Polia legitima* Grote

One specimen collected in '48 in May, pupated on June 11, and adult emerged on July 12.

14. *Lacinipolia meditata* Grt.

Collected in '47 and '50 in May, pupated from July 26 to Aug. 10, and adults emerged from Aug. 24 to Sept. 16. Commonly taken by light trap.

15. *Graptolitha tepida* Grt.

One specimen collected in '50 in June, pupated on Aug. 1, and adult emerged on Sept. 8. Parasites reared from larvae were *Hyposoter annulipes* (Cress.) and *Microplitis* sp. near *autographae* Mues.

16. *Xylena cineritia* Grt.

One adult collected on May 19, '47. Eggs laid on May 21 and hatched on May 28. Larvae pupated on Aug. 22, and adults emerged in October.

17. *Harpaglaea sericea* Morr.

Collected in '50 in May, pupated from Aug. 2 to Aug. 10, and adults emerged from Sept. 9 to Sept. 25.

18. *Eucirrhoedia pampina* Gn.

Collected in '49 and '50 in May and early June, pupated from July 14 to Aug. 8, and adults emerged from Aug. 20 to Sept. 16. Commonly taken by light trap. The parasite *Microplitis confusus* Mues. was reared from this species.

19. *Syngrapha epigaea* Grt.

Collected in '48, '49, and '50 in May and June, pupated from June 6 to July 15, and adults emerged from July 2 to Aug. 8. Eggs laid by one female on Aug. 12, and hatched 6 to 9 days later. Rarely taken by light trap. Parasites reared were *Campoletis* sp., *Apanteles laeviceps* Ashm., *Apanteles longicornis* (Prov.), *Microplitis* sp. near *autographae* Mues., and *Copidosoma truncatellum* (Dalm.).

Geometridae

20. *Scopula* sp., probably *inductata* Gn.

Collected in '49 in May, pupated from June 4 to June 16, and adults emerged from June 21 to July 4. Commonly taken by light trap.

21. *Lygris explanata cunigerata* Wlk.

One specimen collected in '50 in May, pupated on June 23, and adult emerged on July 13. Commonly taken by light trap.

22. *Itame argillacearia* Pack.

Collected in '48, '49, and '50 in May and June, pupated from June 4 to June 30, and adults emerged from June 30 to July 16.

23. *Itame evagaria* Hlst.

One specimen collected in '49 in May, pupated on June 6, and adult emerged on June 23.

24. *Itame fulvaria* Vill.

One specimen collected in '49 in May, pupated on June 6, and adult emerged on June 19.

25. *Xanthotype urticaria* Swett.

Collected in '49 in May, pupated from June 4 to June 6, and adults emerged from June 16 to June 18.

26. *Euchlaena serrata* Dru.

Collected in '48, '49, and '50 in May and early June, pupated from July 1 to July 30, and adults emerged from July 3 to Aug. 5. Commonly taken in light and bait traps.

27. *Euchlaena effecta* Wlk.

Collected in '49 and '50 in May and early June, pupated from June 8 to July 4, and adults emerged from July 1 to July 20.

28. *Euchlaena johnsonaria* Fitch

One specimen collected in '50 on May 24, pupated on June 15, and adult emerged on July 11. Rarely taken by light trap.

29. *Euchlaena vinulentaria* G. & R.

Collected in '49 and '50. Adults emerged on July 12. Rarely taken by light trap.

30. *Cingilia catenaria* Drury

Collected in '48, '49, and '50 (occurred in outbreak number in '49 and '50) from June to end of August, pupated from Aug. 1 to Sept. 18, and adults emerged from Sept. 3 to Oct. 30. Adults mate and oviposit directly after emerging, and winter is passed in the egg stage. Parasites reared were *Itoplectis conquisitor* (Say), *Meteorus cingiliae* Mues., and *Chaetophlepsis orbitalis* Webb.

31. *Lambdina fiscellaria* Guen.

One specimen collected in '50 on July 10, pupated on Aug. 13, and adult emerged on Sept. 9. Rarely taken by light trap.

Pieridae

32. *Colias interior laurentina* Scud.

Collected in '48, '49, and '50 in May and early June, pupated from June 8 to June 21, and adults emerged from June 27 to July 13.

Tortricidae

33. *Archips persicana* Fitch

One specimen collected in '49 in May, pupated on June 4, and adult emerged on July 19.

34. *Sparganothis sulfureana* Clem.

Collected in '48 from July 11 to Aug. 11, and adults emerged from Aug. 12 to Aug. 31. Commonly taken by light trap.

35. *Amorbia humerosana* Clem.

Larvae collected in Sept. '47, and adults emerged in June '48.

36. *Argyrotaenia mariana* Fern.

One specimen collected in Sept. '48, pupated in May '49, and adult emerged on June 2, 1949.

Tineidae

37. *Monopis biflavimaculella* Clem.

Larvae collected in Sept. '47, and adults emerged in August '48. Adults found in the field as early as June 9. Commonly taken by light trap.

Gelechiidae

38. *Aroga trialbamaculella* Cham.

Collected in '49 and '50 in August and September, pupated from May 24 to May 27, and adults emerged from June 9 to June 14. Rarely taken by light trap.

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